SOME WENLOCKIAN FENESTRATE BRYOZOA

by T. G. MILLER

ABSTRACT. *Fenestella rigidula* M'Coy 1850 and *F. lineata* Shrubsole 1880 are considered to be conspecific. Their zooecial chambers are shown to contain structures comparable with the diaphragms of the Trepostomata, and a new genus, *Archaeofenestella*, is erected to contain them. One new species and two new subspecies are described: *Archaeofenestella rigidula polynodosa*, *Fenestella pseudosubantiqua*, and *F. pseudosubantiqua catrionae*. Elias's (1956) suggestion of the presence, in the English Wenlockian, of d'Orbigny's genus *Reteporina* from the Devonian is confirmed. A new genus, *Neoreteporina*, is proposed for certain Carboniferous species described by Nekhoroshev. Finally the polyphyletic nature of the genus *Fenestella* is suggested.

SINCE the validation by the International Commission on Zoological Nomenclature of the generic name *Fenestella* as applied to the well-known Palaeozoic cryptostome bryozoan (*Bull. Zoo. Nom.* 1962), and the designation of a neotype, *Fenestella subantiqua* d'Orbigny 1850, by Elias (1956), I have had the opportunity of examining material from the same locality and horizon in the Holcroft Collection of the Department of Geology in the University of Birmingham, together with type specimens of M'Coy and Shrubsole in the Sedgwick Museum at Cambridge. This study permits certain additions to and modifications of Elias's preliminary assessment of the Wenlockian fenestrate bryozoan assemblage at Dudley.

The lithostratigraphic unit from which this material was collected is the Wenlock Limestone, which occurs at the celebrated collecting locality known as The Wren's Nest, Dudley, near Birmingham. The horizon, in terms of the standard British Silurian succession, is considered (Das Gupta 1933; Butler 1939) to lie at or about the top of the '*Cyrtograptus lundgreni* Zone'. This is probably within the Upper Wenlockian stage VI of Bouček (1953)—i.e. above the zone of *Cyrtograptus rigidus*.

A summary account of some Dudley Wenlockian material in various British collections was included in a review of Palaeozoic Bryozoa published by Nekhoroshev in 1930. This constitutes the only reference to the rich and varied bryozoan assemblage of the Dudley Wenlockian between Shrubsole's 'revision' of 1880 and Elias's of 1956.

Discussion of 'fenestellid' species. In his 1956 paper Elias discussed in detail (1) *Fenestella subantiqua* d'Orbigny; (2) *F. rigidula* M'Coy and *F. lineata* Shrubsole; and (3) *F. reticulata* Lonsdale. It will be convenient to refer to these briefly in the same order.

1. *Fenestella subantiqua* d'Orbigny 1852. It is interesting to note that the Holcroft Collection at Birmingham—which contains large numbers of well-preserved fenestrate bryozoan fragments from The Wren's Nest, Dudley, representing several genera, e.g. *Fenestella*, *Reteporina*, *Semicoscinium*, and *Unitrypa*—does not seem to include an undoubted example of *Fenestella subantiqua* as redescribed by Elias. It is true that, failing the possibility of reference to Lonsdale's holotype, and in view of the extreme fineness with which interspecific discriminations are now made in the fenestrate Bryozoa, it is impossible to be certain to which of the available forms Lonsdale's description referred. This limitation was recognized by Elias (1956, p. 318) when he wrote: '. . . one may

[Palaeontology, Vol. 5, Part 3, 1962, pp. 540–9, pl. 77.]

question whether the selected topotypes truly belong to the species illustrated by Lonsdale. If not, then no specimens from Dudley examined in various collections by Bassler, Duncan, Miller or myself are referable to *F. subantiqua*, and *this species must be extremely rare at Dudley*.' (My italics.) The situation is now clarified in that the neotype material selected by Elias must be taken as the point of reference for any subsequent attribution to *F. subantiqua*.

No. 35 in the Holcroft Collection has gross mesh-dimensions close to those of *F. subantiqua* d'Orbigny emend. Elias, and in certain states of preservation might be confused with that species. In detail, however, it is found that there are differences of specific importance, and I accordingly describe this form below (p. 544) as *Fenestella pseudosubantiqua* sp. nov., together with a new subspecies, *F. pseudosubantiqua catrionae*.

2. *F. rigidula* M'Coy and *F. lineata* Shrubsole. Examination of the type specimens of these species shows that, contrary to Elias's conclusions (1956, pp. 324–9), but in agreement with those of Nekhoroshev (1930), they are conspecific, and Shrubsole's species must therefore be suppressed.

In thin sections cut in the plane of the zoarial expansion an exceedingly important distinguishing feature is seen, namely, the presence, within the zooecial chambers, and occasionally also between them and the median wall, of numerous gently curved and inclined walls or septa passing across from side to side or from side to end (Pl. 77, fig. 4, and text-fig. 1). These structures recall the diaphragms of the Trepostomata, and particularly those of the family Phylloporinidae, which has been assigned tentatively to the Trepostomata by Bassler (1953, p. 116) as '. . . intermediate between Cryptostomata, which it [the family assemblage] resembles in zoarial form, and Trepostomata, which it matches in internal structure'.

Although externally the zoarial mesh of *F. rigidula* is indistinguishable from a 'normal' fenestellid, the presence of internal structures possibly homologous with the diaphragms of the Trepostomata makes it necessary to separate forms in which this morphological feature is developed. I accordingly erect (below, p. 542) the new genus *Archaeofenestella* to accommodate such forms.

3. *F. reticulata* Lonsdale. There remains what is perhaps the most interesting of all the Dudley fenestellids, the form described by Elias (1956, p. 329) as *Fenestella reticulata* Lonsdale. As Elias points out, there seems little doubt that Shrubsole (1880, p. 249) was wrong to erect a new species, *F. reteporata*, distinct from Lonsdale's *F. reticulata*. On the other hand, Nekhoroshev (1930) may have come nearer the truth in supposing that the form described by Lonsdale as *Gorgonia assimilis* is the common large-meshed Dudley fenestellid, in which case the form might seem to be attributable to *Fenestella assimilis* (Lonsdale).

However, there are certain features of the species which make it doubtful whether any attribution to the genus *Fenestella* is correct. This doubt was expressed by Elias (1956, p. 329) when he noted that both Lonsdale and Shrubsole show, in their figures of *F. reticulata* and *F. reteporata* respectively, occasional apertures 'in some carinate dissepiments'; and concludes that 'the occasional lateral contacts of its branches place it close to *Reteporina* (=?*Semicoscinium*)'.

Examination of thin sections of examples of this form from the Dudley Wenlockian (H:26 and H:10) shows that some of the so-called 'dissepiments' are parts of normal zooecia-bearing branches, in which deflection of growth-direction has apparently led to

branch anastomosis. In other cases only half a 'dissepiment' contains cells, while the other half completes an inter-branch linkage with the massive calcareous tissue of a normal dissepiment. When an 'abortive' branch-division forms part of a 'pseudo-dissepiment', the resulting structure is irregular in shape, the cell-bearing part usually projecting into the fenestrule, so that the fenestrule is roughly heart-shaped. In a single zoarium, or zoarial fragment, every gradation can be seen, from cases of extremely short, wide dissepiments at points where branches almost touch, to comparatively long dissepiments, without cells. In the latter case there is often enlargement of the zooecial chambers opposite the point of insertion of the dissepiment in the branch, and abnormally constricted cells project from the branch into the dissepiment.

The obverse of the branches shows, instead of a fenestellid 'carina', a steep-sided but apically rounded axial surface above the zooecial apertures, and no 'carinal' nodes. The line of separation between the main skeletal material and the external 'sclerenchymal' investment is not sharp. The external investment itself contains, or is partly constructed of, a mass of small, isolated tubular (or possibly rod-like) bodies, arranged more or less radially with respect to the branch and 'dissepiment' cross-sections, and normal to the fenestrule sides.

These characters make it impossible to assign the form under discussion to the genus *Fenestella* Lonsdale 1839.

Nekhoroshev (1956, pp. 173–83) has discussed the genus *Reteporina* at considerable length. Bassler (1953, p. 126) described it as 'poorly known; may be senior synonym of *Semicoscinium*'. Some of Nekhoroshev's figures (e.g. pl. 27, figs. 1, 2) of *Reteporina altaica e*, and *R. altaica major*, from the Lower Carboniferous of the Altai, are at first sight similar in general appearance to Lonsdale's species, although in detail the dimensions are of course different. The resemblance is less marked in the outline drawings of thin sections (e.g. pl. 28, figs. 1–10). Nowhere in this series of drawings does Nekhoroshev show a true anastomosis of branches. Although in fig. 8*a* he shows branches almost touching each other, there is no case of a row of zooecial chambers passing uninterruptedly from one branch to another. D'Orbigny's diagnosis (quoted by Nekhoroshev 1956, p. 173) explicitly states that anastomoses are present: '. . . branches largement anastomosées de manière a ne laisser entre elles que des oscules oblongs, réguliers, placés par lignes divergentes'.

It must be concluded, therefore, that the Dudley Wenlockian '*Fenestella*' *reticulata* should properly be assigned to *Reteporina* d'Orbigny 1849, erected for a Devonian example; and that Nekhoroshev's Carboniferous species must be ascribed to a separate genus, *Neoreteporina* (which I define below, p. 547), morphologically intermediate between *Reteporina* and *Fenestella*, and probably related to *Levifenestella* Miller 1961*b*.

SYSTEMATIC DESCRIPTIONS

Specimens from the Sedgwick Museum, Cambridge, are prefixed SM; those from the Department of Geology, University of Birmingham, are prefixed BU.

Order CRYPTOSTOMATA Shrubsole and Vine 1882

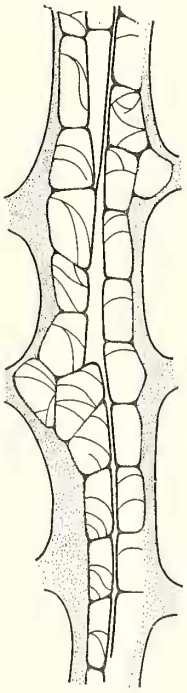
Family FENESTELLIDAE King 1850

Genus ARCHAEOFENESTELLA gen. nov.

Type species: Fenestella rigidula M'Coy (1850, p. 288), Silurian, England.

Diagnosis. Zoarium of branches and dissepiments arranged to form a reticulate 'fenestellid' mesh. Branches with a straight internal median wall separating two rows of zooecial chambers opening on the obverse of the zoarium, and externally with a prominent median carina which bears nodes. Zooecial chambers rectangular or rhomboidal in base shape, divided internally by transverse diaphragm-like walls in the posterior part of the chamber.

Discussion. The genus is distinguished from *Fenestella* by the presence of diaphragm-like dividing walls within the zooecial chambers (and occasionally between them), and by the straightness of the median wall dividing the branches, which allows the zooecial chambers on each side to follow each other without alternation with their neighbours on the other side of the wall. In all other respects, and particularly in the gross form of the zoarial expansion, there seems to be no difference from *Fenestella.* However, the internal zooecial septa, which recall the internal structure of the zooecia in *Subretepora*, and which are not present in any other genus of the Fenestellidae, must reflect some fundamental distinguishing feature in the zooid. The presence of apparently similar structures in members of the mainly Ordovician family Phylloporinidae suggests that the structure should be regarded as 'primitive' in terms of bryozoan phylogeny.



TEXT-FIG. 1. Semi-diagrammatic drawing of branch structure in *Archaeofenestella* showing septal traces within the zooecial chambers. (From a thin section of *A. rigidula*; notional magnification ×45.)

Archaeofenestella rigidula (M'Coy)

Plate 77, figs. 1, 4; text-fig. 1

Fenestella rigidula M'Coy 1850, p. 288.
Fenestella rigidula M'Coy; M'Coy 1855, p. 50.
Fenestella rigidula M'Coy; Shrubsole 1880, p. 248.
Fenestella lineata Shrubsole 1880, p. 249.
Fenestella rigidula M'Coy; Nekhoroshev 1930, p. 185.
Fenestella rigidula M'Coy; Elias 1956, p. 327.

Material:

1. *A. rigidula* (M'Coy), holotype, SM. A:10111, Wenlock Limestone, Dudley, Staffordshire (*sic.*).
2. *Fenestella lineata* Shrubsole, holotype, SM. A:10210, Wenlock Limestone, Dudley, Worcestershire.
3. Topotypes BU. H:39 and H:40, Wenlock Limestone, Wren's Nest, Dudley, Worcestershire.

Micrometric formulae:

	B/10	D/10	Z/5	N/5	B_w	ZD	ZB
SM. A:10111	20–22	15–17	26–28	16–25	0·25	0·10	rh.
SM. A:10210	20–28	13–16	24–30	17–22	0·25	0·10	rh.
BU. H:39	22	18	30	?	0·25	0·10	rh.
BU. H:40	21	14–15	28–30	12–14	0·25	0·10	rh.

[B/10—no. of branches in 10 mm. across the zoarium; D/10—no. of dissepiments in 10 mm. along the branches; Z/5, N/5—no. of zooecial apertures and carinal nodes in 5 mm. along branches; B_w—width

of branches in mm.; ZD—diameter of zooecial apertures in mm.; ZB—shape of main part of zooecial chamber in plane of zoarial expansion; rh.—rhomboidal; rect.—rectangular.]

Description. Normal reticulate fenestellid mesh of bifurcating branches and transverse dissepiments. Branches markedly straight and parallel, bearing rather large 'collared' zooecial apertures, less than their own diameter apart. Occasionally an abnormally large cell-aperture is placed opposite the end of a dissepiment. Reverse of branches with prominent longitudinal ribs. In thin section in the plane of the expansion the zooecial chambers are seen to be set in two rows within the branches, the rows separated by a straight central dividing wall, each cell-base having the shape of a parallelogram. The cells are divided internally by transverse, gently curved septa, usually two, but in some cases up to four in a cell (text-fig. 1; Pl. 77, fig. 4). In both branches and dissepiments scattered 'tubules' occur. These lie generally normal to the axis of the branch or dissepiment.

Archaeofenestella rigidula polynodosa subsp. nov.

Material: Syntypes BU. H:24 (ii), and H:45, Wenlock Limestone, Dudley, Worcestershire.

Micrometric formulae:

BU. H:24 (ii), H:45.	22–24	16–18	26–29	26–30	0·15–0·25	0·10–0·13	rh.
F. lineata Elias 1956	18–24	12–15	26–27	25–27	?	?	?
A. rigidula M'Coy	20–22	15–17	26–28	*16–25*	0·25	0·10	rh.

Discussion. This form is exceedingly close to *A. rigidula* (M'Coy) except in the somewhat greater density of carinal nodes. It may be the form described by Elias (1956, p. 324) as *Fenestella lineata* Shrubsole.

Genus FENESTELLA Lonsdale 1839

Fenestella pseudosubantiqua sp. nov.

Plate 77, fig. 3

Material: Holotype BU. H:35, Wenlock Limestone, Dudley, Worcestershire.

EXPLANATION OF PLATE 77

All specimens from Wenlock Limestone, Dudley, Worcestershire.

Fig. 1. *Archaeofenestella rigidula* (M'Coy). Holotype SM. A:10111. Part of obverse of zoarial expansion in which zooecial septa have been exposed by weathering, ×25.

Fig. 2. *Reteporina reticulata* (Lonsdale). BU. H:26. Polished and etched surface showing arrangement of zooecial chambers within the branches, and 'abortive' branch-divisions forming pseudo-dissepiments, ×14.

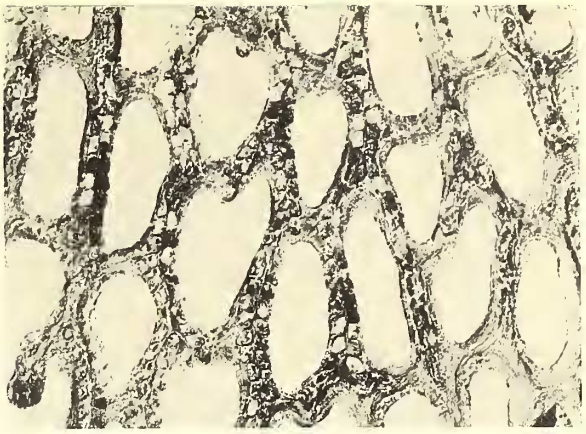
Fig. 3. *Fenestella pseudosubantiqua* sp. nov. Holotype BU. H:35. Part of reverse of zoarial expansion. The upper half of the fragment has been removed to show (as dark spots) the impressions of the prominent widely-spaced carinal nodes, ×8.

Fig. 4. *Archaeofenestella rigidula* (M'Coy). SM. A:10210 (labelled *Fenestella lineata* Shrubsole—holotype). Thin section in plane of zoarial expansion showing rhomboidal zooecial base-shape and internal transverse septa, ×20.

Fig. 5. *Reteporina reticulata* (Lonsdale). BU. H:10. Part of reverse of zoarial expansion, ×8.

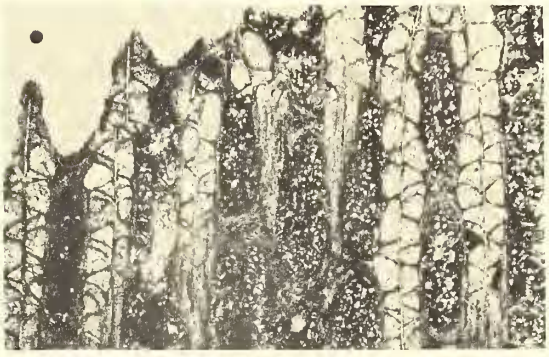
Fig. 6. *Reteporina reticulata* (Lonsdale). BU. H:26. Thin section of branch showing zooecial chambers and median wall, ×70.

1



2

3



4

5

6

MILLER, Wenlockian fenestrate Bryozoa

Micrometric formulae:

Holotype BU. H:35	16–18	9	20–29	8–11	0·15–0·20	0·10	rh.
cf. *F. subantiqua* d'Orbigny 1852, emend. Elias 1956	16–19	9–11	25–26	*c. 25–26*	?	?	?

Description. Normal, regular fenestellid mesh of slender, slightly flexuous branches with transverse dissepiments. The gross dimensions of the zoarial elements closely resemble those of *F. subantiqua* d'Orbigny as redescribed by Elias (1956), except for the presence in the new species of relatively stout straight-sided cylindrical carinal nodes widely spaced along the carina.

Fenestella pseudosubantiqua catrionae subsp. nov.

Material: Holotype BU. H:24 (i), Wenlock Limestone, Dudley, Worcestershire.

Micrometric formula:

Holotype BU. H:24 (i)	16–20	13–16	26–28	7–10	0·20–0·25	0·10	rh.

Discussion. This form differs from *F. pseudosubantiqua* in having slightly straighter, stouter, branches, and almost square rather than oblong fenestrules.

Genus RETEPORINA d'Orbigny 1849 emended

Type species: Reteporina prisca (Goldfuss 1826), Middle Devonian, Germany.

Emended diagnosis. Zoarium of irregularly flexuous, relatively stout, non-carinate, occasionally anastomosing branches with some transverse dissepiments. Fenestrules correspondingly large, elongated and irregular. Zooecial chambers with rectangular base-shape and small apertures directed towards one side of the zoarial expansion only. Investing tissue compounded of densely packed minute rods or 'tubules' in a fibrous calcareous 'matrix'.

Discussion. There seems to be no question of the possible identity of this genus with *Semicoscinium* Prout 1859 (as suggested tentatively by Bassler 1953, p. 126), since the latter genus is distinguished by the prominent expansion of the upper part of a well-developed median carina on the obverse of its branches. In *Reteporina* the branches, although rising to a rounded crest, have no distinct carina.

Reteporina reticulata (Lonsdale)

Plate 77, figs. 2, 5, 6; text-fig. 2

Retepora reticulata Lonsdale 1839, p. 678.
Gorgonia assimilis Lonsdale 1839, p. 680.
Fenestella reteporata Shrubsole 1880, p. 249.
Fenestella assimilis (Lonsdale); Nekhoroshev 1930, p. 184.
Fenestella reticulata Lonsdale; Elias 1956, p. 329.

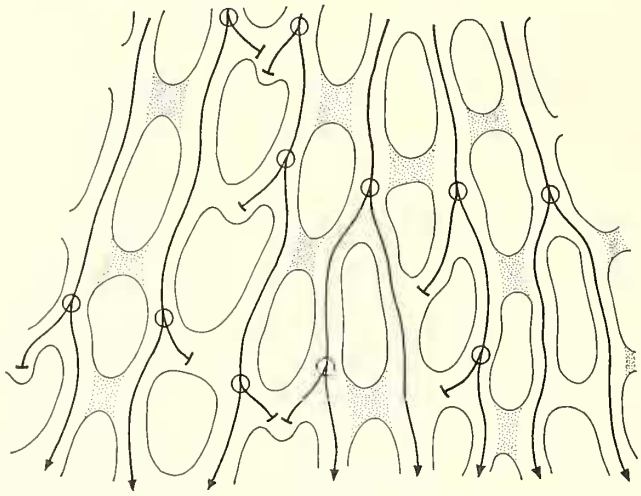
Material: Specimens BU. H:10 and H:26, Wenlock Limestone, Dudley, Worcestershire.

Micrometric formula:

Specimens BU. H:10 and H:26	10–12	4–5	19–23	0	0·3–0·5	0·125	rect.

Description. Irregular to subreticulate mesh of stout flexuous bifurcating and anastomos-

ing cell-bearing branches occasionally joined by oblique or transverse dissepiments which may also bear cells either throughout their length, or in part only. The branches do not carry, on the obverse, a distinct carina, but their sides rise fairly steeply to a rounded crest. There are no carinal nodes. Each branch is divided by a central, slightly flexuous longitudinal wall into two parts occupied by a regular line of zooecial cells. The cells have rectangular bases and relatively small apertures emerging at the end of long vestibules. The appearance of true dissepiments is sometimes achieved by the effect



TEXT-FIG. 2. Diagram of branch-division structure in relation to dissepiments and pseudo-dissepiments in *Reteporina*. The branch growth-direction is indicated by heavy arrowed lines, and terminations of 'abortive' branches by cross-bars. Dissepiments are stippled. (Notional magnification ×15.)

of bifurcating branches which on approaching neighbouring branches have become united to them by an outgrowth of investing tissue. Part of the 'pseudo-dissepiment' is cell-bearing in such a case, and part not. In other cases true dissepiments have developed where the bending of adjacent branches has almost brought them into contact. In yet other cases one branch appears to have grown straight into another without interruption of cell arrangement. Fenestrules sometimes irregularly heart-shaped near cell-bearing pseudo-dissepiments resulting from abortive branch division. The zooecial chambers or cells occasionally contain a single, obliquely transverse, septum.

Discussion. Nekhoroshev (1956, pp. 173–85) has described a well-developed assemblage, in the Lower Carboniferous rocks of the Altai, as *Reteporina altaica* vars. *a*, *b*, *c*, *d*, *e*, and *major*, and *R. minima*. Although all these forms show the characteristic reteporinoid flexuosity of branches, none of them appears, from Nekhoroshev's photographs and drawings, to have truly anastomosing branches or cell-bearing dissepiments. Instead, wide non-celluliferous dissepiments are developed wherever branch bending brings two neighbouring branches almost into contact. Moreover, in some of the varieties, particularly var. *a*, the number of zooecial apertures is reduced to only three or four to a fenestrule; while in others, for example *c*, *d*, and *e*, a distinct carina can be seen on the branches, with a suggestion (in var. *e*) of carinal nodes. It seems unlikely,

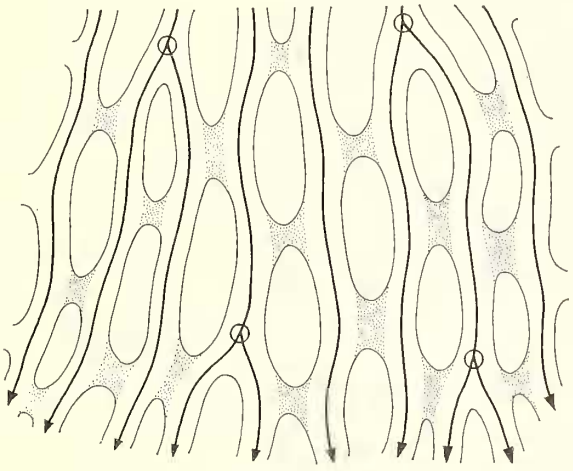
therefore, that Nekhoroshev's species can properly be assigned to *Reteporina*, although they are sufficiently distinct from species of *Fenestella* to be excluded from that genus. I therefore propose to transfer these Russian species to a new genus, *Neoreteporina*.

Genus NEORETEPORINA gen. nov.

Text-fig. 3

Type species: Reteporina altaica Nekhoroshev (1956, p. 177, pls. 26–28), Lower Carboniferous, Russia.

Diagnosis. Like *Reteporina*, but with a more regular meshwork, without cell-bearing dissepiments and true anastomosis of branches, and with an incipient carina on the obverse of the branches, but no carinal nodes.



TEXT-FIG. 3. Diagram of branch structure in relation to dissepiments in *Neoreteporina*. The branch growth-direction is indicated by heavy arrowed lines. Dissepiments are stippled. (Composite drawing after Nekhoroshev 1956, pl. 28, figs. 1–7; notional magnification ×15.)

CONCLUSION

The presence, in English Silurian strata, of the genus *Reteporina*, together with a 'primitive' representative of the main fenestellid stock, here distinguished as *Archaeofenestella*, and apparently 'normal' members of the genus *Fenestella*, has some bearing on currently accepted notions of the phylogeny of the Fenestellidae.

Nekhoroshev (1928, p. 505, fig. 9) suggested the more or less 'explosive' derivation of six fenestellid genera from a main *Fenestella* stock during the Silurian period. These genera were *Polypora*, *Helicopora*, *Ptiloporella*, *Fenestralia*, *Semicoscinium*, and *Hemitrypa*. The main *Fenestella* stock was shown as associated rather tentatively with the development in early Ordovician times of *Chasmatopora* (now ascribed to *Subretepora*), a little-known Phylloporinid genus.

There seems little doubt that members of the family Fenestellidae could be derived on purely morphological grounds from several members of the Phylloporinidae, e.g.